

Disadvantages of Preferential Dispersals in Fluctuating Environments

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(Dated: February 27, 2014)*

It has not been known whether preferential dispersal is adaptive in fluctuating environments. We investigate the effect of preferential and random dispersals in bet-hedging systems by using a discrete stochastic metapopulation model, where each site fluctuates between good and bad environments with temporal correlation. To explore the optimal migration pattern, an analytical estimation of the total growth is derived by mean field approximation. We found that the preference for fertile sites is disadvantageous when transportation among sites has a cost or the sensitivity of preference is high.

Bet-hedging is a risk spreading strategy that increases a population's fitness in the face of fluctuating environments [1–7]. For example, consider offspring allocation into two sites, either of which is so poor that the population cannot survive without dispersal [8, 9]. The random dispersal between two sites can lead to population persistence. Also in finance, diversified investment is a key point for risk mitigation [10]. To increase expected returns, the wealth should be invested into a wide variety of assets. In these bet-hedging models, random dispersal is assumed.

However, in the case that the environment of each site fluctuates with temporal correlation, it is not clear whether the random dispersal is the best strategy as bet-hedging. There is a possibility that the preferential dispersal improves the growth of a population. If the environment has a temporal correlation, a large population implies that environment tends to remain good subsequently. Therefore, for an individual changing the habitat, it is advantageous to choose populous sites than sparsely populated ones. However, what is good for individual is not necessarily good for a whole.

In this paper, we study a stochastic metapopulation which is given as a discrete-time stochastic matrix model [11, 12]. In these studies, to evaluate the population's fitness for this class model, the total growth was calculated approximately. Assuming random dispersal, the preferential dispersal has not been taken into consideration. Here, we introduce a simple model with preferential dispersal and present the mean-field theory for the model. The purpose of this paper is to compare the total population growths between preferential and random dispersals.

Let us consider population that inhabits in n discrete sites. Let $x_i(t)$ be the number of individuals in site i ($1 \leq i \leq n$) at time t . Thus, the sum of populations in all sites

is

$$S(t) = \sum_{i=1}^n x_i(t). \quad (1)$$

The initial condition is set as $x_i(0) = 1$, i.e., $S(0) = n$. In each site, the population reproduces with random growth $m_i(t)$, which are stochastic variables with finite variance. The probability distributions of $m_i(t)$ are assumed to be the same for all sites. The total growth is given as

$$\bar{m}(t) = \frac{1}{S(t)} \sum_{i=1}^n m_i(t)x_i(t). \quad (2)$$

Thus,

$$S(t+1) = \bar{m}(t)S(t). \quad (3)$$

We assume that all sites are connected to one another, and a proportion q of the population tries to migrate at each time step. The remaining population stays at the same site. Thus, the population dynamics is written as

$$x_i(t+1) = (1-q)m_i(t)x_i(t) + q\bar{m}(t)S(t)F(\{x_i(t)\}), \quad (4)$$

where q represents the migration rate, $q\bar{m}(t)S(t)$ is the number of population that migrates, and $F(\cdot)$ represents the preference of migration. We assume that a fraction r of the migrating population tends to be attracted to fertile sites and the remain moves at random. Then, we have

$$F(\{x_i(t)\}) = r \frac{m_i x_i(t)}{\bar{m}(t)S(t)} + (1-r) \frac{1}{n}. \quad (5)$$

The first term of the right hand side of this equation means that the fraction r of the migrating population

selects sites with the probability linearly proportional to the population. In summary, each individual stays the same site with the probability $(1 - q)$, migrates preferentially with the probability qr , and migrates randomly with the probability $q(1 - r)$. Summing (4) over all sites, we obtain (3), again. Let us denote the relative population size by

$$y_i(t) = \frac{x_i(t)}{S(t)}. \quad (6)$$

Dividing both sides of (4) by both sides of (3) and using (5), the dynamics of the relative population size $y_i(t)$ is obtained

$$y_i(t+1) = \frac{m_i(t)}{\bar{m}(t)}(1 - q + qr)y_i(t) + \frac{1}{n}q(1 - r). \quad (7)$$

Since eq. (2) is rewritten as

$$\bar{m}(t) = \sum_{i=1}^n m_i(t)y_i(t), \quad (8)$$

the stochastic process (7) describes the evolution of $y_i(t)$ completely. It is obvious that the condition $\sum_{i=1}^n y_i(t) = 1$ is conserved for the dynamics (7).

For simplicity, the local growth $m_i(t)$ is assumed to take one of two values, m_- with probability p and m_+ with probability $1 - p$. Here, we set $m_+ > m_-$. The stochastic fluctuation of the local growth comes from environmental fluctuations. The cases of m_+ and m_- are called good and bad environments, respectively. Here, we take into account temporal correlation of $m_i(t)$. We introduce the autocorrelation function

$$R(\tau) = \langle m_i(t)m_i(t+\tau) \rangle - \langle m_i(t) \rangle \langle m_i(t+\tau) \rangle \quad (9)$$

that decays exponentially

$$R(\tau) \propto \exp(-\tau/\tau_c), \quad (10)$$

where τ_c is an autocorrelation time. To obtain a stochastic time series satisfying the property (10), we use Markov chain with transition probability matrix

$$P_{env} = \begin{pmatrix} 1 - pu & pu \\ (1 - p)u & 1 - (1 - p)u \end{pmatrix}, \quad (11)$$

where

$$u = 1 - \exp(-1/\tau_c). \quad (12)$$

For example, the first row and second column element of the matrix P_{env} represents the probability that a site changes from good to bad. Here, we neglect spatial correlation of the local growth $m_i(t)$ for simplicity.

Before analyzing the model, we remark that since the stochastic process (7) depends on q and r only through the form $q(1 - r)$, the solution of (7) is identical for the

same values of $q(1 - r)$. Thus, it is convenient to introduce a new combined parameter

$$\phi = q(1 - r). \quad (13)$$

Now, we develop the mean-field approximation for the model. The ratios of population in the two environments are denoted as $\rho_+(t)$ and $\rho_-(t)$, respectively. Here, $\rho_+(t) + \rho_-(t) = 1$ and the total growth is given as

$$\bar{m}(t) = m_+\rho_+(t) + m_-\rho_-(t). \quad (14)$$

The evolution of $(\rho_+(t), \rho_-(t))$ is described by

$$(\rho_+(t+1), \rho_-(t+1)) = \left(\frac{m_+}{\bar{m}(t)}\rho_+(t), \frac{m_-}{\bar{m}(t)}\rho_-(t) \right) P_{all}. \quad (15)$$

Here, the term P_{all} is defined

$$P_{all} = (1 - q)P_{env} + q(1 - r)P_{rand} + qrP_{pref}P_{env}, \quad (16)$$

where

$$P_{rand} = \begin{pmatrix} 1 - p & p \\ 1 - p & p \end{pmatrix} \quad (17)$$

and

$$P_{pref} = \frac{1}{\bar{m}(t)} \begin{pmatrix} m_+\rho_+(t) & m_-\rho_-(t) \\ m_+\rho_+(t) & m_-\rho_-(t) \end{pmatrix}. \quad (18)$$

The first term of the right hand side of (16) stands for the case that the individual continues to stay at the same site and the environment changes. The second term of (16) stands for the case that the individual moves randomly. The first (second) column of matrix P_{rand} is the probabilities that the environments in the end of the migration is good (bad). The final term of (16) stands for the case of preferential dispersal. The first (second) column of matrix P_{pref} is the probabilities that the environments in the end of the migration is good (bad).

This approximation is true in the limit of $n \rightarrow \infty$. A stationary solution $\rho_+ = \rho_+(t+1) = \rho_+(t)$, is obtained analytically by working out (15). Because P_{all} and $\bar{m}(t)$ depend on $\rho_+(t)$ and $\rho_-(t)$, we need to solve a quadratic equation. By solving (15), the expected value of the total growth is expressed as

$$\bar{m} = m_+\rho_+ + m_-\rho_-, \quad (19)$$

where ρ_+ and ρ_- are its solutions. In the absence of temporal correlation ($\tau_c = 0$), (19) is rewritten as $\bar{m} = m_+(1 - p) + m_-p$. In this case, the total growth is independent of q and r . On the other hand, if $\tau_c \neq 0$, the total growth takes an intricate form.

Figure 1 shows the dependence of total growth rate $\log \bar{m}$ of q and r . The time average of $\log \bar{m}$ is calculated numerically in the case of $\tau_c = 1$ (see Fig. 1(a)). As we showed theoretically, the population has the same

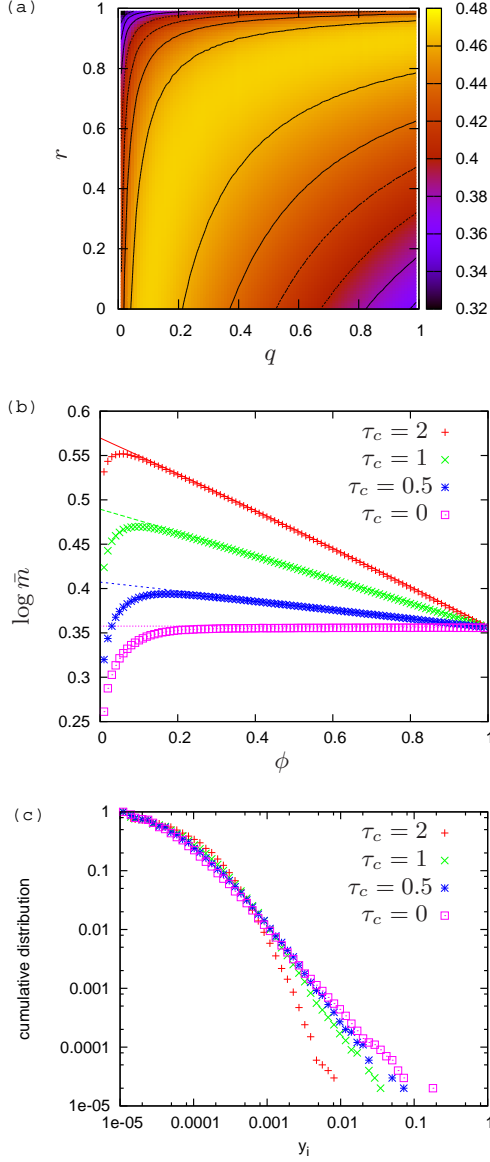


FIG. 1. (a) The dependence of the population's fitness of q and r . The average of total growth rate $\log \bar{m}$ is calculated by numerical simulation for 10,000 time steps over a transient of 10,000 time steps, when $\tau_c = 1$. The plots are given by the average over 100 stochastic realizations. The other parameters are set as $m_+ = 2$, $m_- = 0.1$, $p = 0.3$, $n = 100$. (b) The average of total growth rate of as a function of $\phi = q(1 - r)$ for three values of autocorrelation time $\tau_c = 0, 0.5, 1, 2$. The crosses represent the numerical result for $r = 0$. The curves give the prediction by the mean-field approximation. (c) Log-log plots of the cumulative distributions of the relative population y_i for $q = 0.1$ and $n = 10,000$. We find that the tail of the distribution is lighter for stronger correlation.

growth rate when $\phi = q(1 - r)$ is identical. There is a finite optimal value of $\phi = q(1 - r)$, where the total growth rate has the maximal value (see Fig. 1(a)). Figure 1(b) compares the time average of $\log \bar{m}$ obtained by the numerical simulation with the mean-field approximation for some values of τ_c (19). The mean-field approximation indicates that the total growth rate is a decreasing function of $\phi = q(1 - r)$ for $\tau_c > 0$. If ϕ is not near 0, the numerical result agrees with the mean-field approximation very well. On the other hand, for small ϕ , the numerical average for $\log \bar{m}$ is smaller than the prediction. The reason for this deviation is as follows. If ϕ (also q) is near 0, the distribution of the relative population size $y_i(t)$ has a heavy tail and the fluctuation of \bar{m} is not negligible. When the fluctuation of $\bar{m}(t)$ increases, the time average of $\log \bar{m}(t)$ grows more smaller than the logarithm of the mean value of $\bar{m}(t)$ [12]. As a result, if the environment has time correlation ($\tau_c > 0$), there is a finite optimal value of ϕ . When the correlation time becomes longer, the distribution's tail of $y_i(t)$ is lighter (see Fig. 1(c)) and the deviation from the mean-field approximation becomes smaller. Thus, the optimal value of ϕ decreases as τ_c increases, as seen in Fig. 1(b).

The result in Fig. 1(c) appears to be in contrast to the previous works on Langevin systems with colored multiplicative noise, where the distribution's tail is heavier due to temporal correlation [13, 14]. We focus on the simultaneous distribution of metapopulation coupled by migration, while the previous works dealt one-dimension stochastic process. In our case, the temporal correlation tends to level off the populations over all sites.

Because of the degenerate character of the model, the optimal values of q and r cannot be decided uniquely. Here, we expand the model to resolve the degeneracy in two ways. First, we take into account a cost of migration between sites. Introduce the survival rate $s < 1$, by which the second term of the right hand side of (3) is multiplied. In this case, the total growth rate is smaller than the one in the original model, when $q > 0$. The difference between these two values increases with the migration rate q . As a result, the values of r for the optimal migration is zero. Figure 2(a) shows the numerical plot of the average of $\log \bar{m}$ for $s = 0.95$. In this case, the preference for fertile sites is not advantageous.

Second, we consider the case that the sensitivity of the preference is higher. We assume that the migrating individuals follow

$$F(\{x_i(t)\}) = r \frac{[m_i x_i(t)]^\alpha}{\sum_{j=1}^n [m_j x_j(t)]^\alpha} + (1 - r) \frac{1}{n}, \quad (20)$$

instead of (5). Here, the exponent α represents the sensitivity of preference. Figure 2(b) shows the numerical plot of the average of $\log \bar{m}$ in the case that the preference is superlinear ($\alpha > 1$). As seen in Fig. 2(b), the optimal value of r is zero, again. In the case of higher

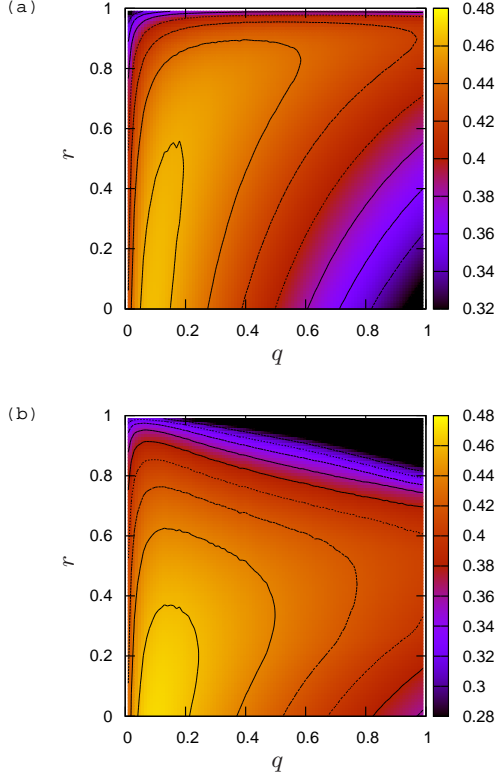


FIG. 2. The total growth rate $\log \bar{m}$ for two expanded cases as a function of q and r . (a) The case that transportation between sites has a cost. The survival rate during the transportation is set to be $s = 0.95$. (b) The case that the preference is superlinear in the population, where migrating individuals select sites with the probability proportional to the square of the population size. The black region means that the total growth rate is smaller than the minimum value of the right color bar. The other parameters are the same as in Fig. 1(b).

sensitivity, because the population is excessively concentrated to particular sites, bet-hedging cannot work well. Conversely, if the preference is sublinear ($\alpha < 1$), the preference is favored. Consequently, a high sensitivity makes the preference disadvantageous.

Up to here we have investigated a stochastic metapopulation model in fluctuating environments by comparing preferential dispersal and random dispersals. We showed that when the correlation time of the environments increases, the optimal value of $\phi = q(1 - r)$ decreases, i.e., the migration rate q decreases for a given r , and the strength of the preference r increase for a given q . Moreover, if the migration has a cost or the sensitivity

of preference is high, then random migration is favored compared with preferential migration. These results are robust to variations the environmental parameters m_+ , m_- , p . If we consider other shrewd preferences, we may find the case that the preferential dispersal is advantageous.

There are similar studies that genetically clonal populations in fluctuating environment [15, 16]. They contrasted two types of phenotype switchings: responsive switching and spontaneous random switching [15, 16]. These studies showed that random switching is favored rather than responsive switching in many cases. The principle derived here may be the same with the above phenotype switchings. We would like to emphasize that the principle we obtained here may provide a reference for future research. Since the bet hedging systems have been studied widely in ecology, evolution and economics, we believe that our approach will be widely useful.

This work was supported by grants-in-aid from the Ministry of Education, Culture, Sports, Science and Technology of Japan to S.M. (No. 24500273) and J. Y. (No. 22370010 and No. 22255004). A part of the numerical computation in this work was carried out at the Yukawa Institute Computer Facility.

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